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Journal of Theoretical Biology 240 (2006) 14–23
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

A mathematical consideration for the optimal shell change of hermit crab

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Received 21 February 2005; received in revised form 26 July 2005; accepted 22 August 2005
Available online 29 September 2005

Abstract

Shell of the adult hermit crab has some important roles for its fitness. In the same time, the shell size often limits the body growth of its owner. To grow the body size larger, the individual must change the shell to another larger shell. If the individual cannot get another larger one, the individual has to suppress the body size growth as the occupied shell size allows. Growth suppression would result in the lower fitness. With a simple mathematical model, we consider the criterion about whether the individual should try to change the shell or not in order to get the higher fitness. We show that the optimality of a shell change behavior has a relation with the body size and the season length for the shell change. They also affect the optimal timing for the shell change. It is implied that the probability of the success in a shell change and the cost for the shell change behavior do not affect the optimal timing for the shell change at all but significantly do the optimality of the behavioral choice.

Keywords: Hermit crab; Optimal behavior; Optimal timing; Body size; Mathematical model

1. Introduction

About 800 species of hermit crabs carry empty snail shells as their shelter (Hazlett, 1981; Kuhlmann, 1992; Angel, 2000; Rotjan et al., 2004). In general, the hermit crab grows up to adult after the period of zoea floating in seawater like planktons. Zoea period is 2–5 weeks for the species of the shallow sea. Although the adults are terrestrial, they move to sea for hatching eggs. After several molts in the zoea period, the individual seeks a shell. Only such individual that succeeds in getting its shell can grow up to adult and can increase the body size after several shell changes (Reese, 1962; Hazlett, 1981; Rotjan et al., 2004).

Some species show the reproductive activity throughout year, and the others do only in some specific months. For example, *Calcinus laevimanus* in Hawaii shows a reproductive behavior throughout year except for the period from November to February, while *Clibanarius zebra* inhabiting in the same region breeds almost just in August (Reese, 1963).

How could the hermit crab get a new shell? We can observe two types of behavior. The first is to obtain a shell just after the snail dies, that is, a vacant shell. In general, such a shell after the snail's death is buried, destroyed and swept away by waves. Even though a hermit crab can encounter such a shell, it may not meet its requirement. The second is to obtain a shell which another crab has, that is a ritualizing behavior. Attacker hermit crab rocks, shakes, and rapps the defender. When the defender gives up its shell, the attacker quickly gets into the defender's shell, and at the same time the ejected defender gets into the attacker's one. In a sense, two crabs exchange the shells from each other (Hazlett, 1981).

A merit to carry the shell is the defense against predators (Hazlett, 1981; Kuhlmann, 1992; Angel, 2000; Rotjan et al., 2004). When a predator comes near, the hermit crab pulls its body into the shell and covers the shell with its claw. Individual with a small shell is much likely subjected to the predation, for instance, by fish (Hazlett, 1981). The shell contributes to the tolerance against some physical

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0022-5193/$ - see front matter
doi:10.1016/j.jtbi.2005.08.019

stresses, too (Reese, 1969). In some cases, hermit crabs die for the desiccation or the change of osmotic stress. Species inhabiting in the high intertidal region utilizes the shell to retain sufficient water in it (Bertness, 1981b).

Another merit of the shell is to increase the reproductive success. For female, the shell is to guard its eggs. Some decapod crustacea have difficulty to move with keeping own eggs under the abdomen, whereas the shell is beneficial for the egg protection against predation and physical stresses. As for the reproduction success, the larger shell makes it easier for male to grip the female and guard her from the other males. In the case when male hermit crabs contend for a female, the male with the larger shell could get advantage against the other with the smaller.

On the other hand, the hermit crab has some disadvantages due to keeping the shell. Carrying it requires the cost, although it is beneficial for its survival. Actually, the oxygen consumption by *Coenobita compressus* without shell is estimated to be 67% of that with a shell (Herreid and Full, 1986).

Besides, even when an individual seeks a new shell, it could not always get an appropriate one. Even when the shell becomes damaged or unsuitable for growing the body size, it is in general not easy to find and obtain an appropriate another one. Indeed, the shell selection of hermit crab usually occurs after a lengthy period of investigation (Neil and Elwood, 1986; Brown et al., 1993; Côté et al., 1998; Benvenuto and Gherardi, 2001). It is suggested that some individuals should have to restrict the growth of body size even when there would be enough food to grow up the body size (Markham, 1968; Childress, 1972; Bach et al., 1976; Fotheringham, 1976; Bertness, 1981a; Floeter et al., 2000).

The shell size could limit the reproductive success (Childress, 1972; Bertness, 1981a, b; Hazlett, 1989; Hazlett and Baron, 1989; Elwood et al., 1995; Côté et al., 1998; Floeter et al., 2000). For female, the shell size determines the total amount of eggs that could be kept in the shell. For male, the smaller individual with the smaller shell could get the less opportunity for successful mating than the larger one could (Childress, 1972; Bach et al., 1976; Fotheringham, 1976, 1980; Bertness, 1981a). For several tropical species, it is observed that berried females are with inadequate shell (Bertness, 1981a, b).

The shell is closely related to the survival and the reproductive success of hermit crab. From the viewpoint of the survival or/and the reproductive success, what is the best timing for the shell change? What condition is required for the case that the individual could expect the greater advantage from the suppression of body size growth without changing the shell than from the body size growth with changing the shell? In this paper, we will consider these problems with a mathematical modeling, focusing how the strategy to get the maximal reproductive success depends on the body size and the season length for a shell change. As far as we could have known, our work would be a pioneer one with a mathematical model about these problems.

2. Assumptions

2.1. Body size

Body size of hermit crab is a function of time. If an individual could use the larger shell, the body size grows up to the larger size as long as the occupied shell could allow.

2.2. Shell change

We assume that the individual could take such a behavior as to change the shell to the larger one except in the breeding season. That is, the individual can choose the behavior of the shell change only in the period between two subsequent breeding seasons, say, *the inter-breeding season*. Furthermore, it is assumed that the individual could change the shell only once in each inter-breeding season. In our modeling, the length of inter-breeding season is given by a constant T. In reality, the cycle of hermit crab's shell changes is not well known (Gilchrist, 2003). However, in this paper, according to the shell change, we focus on the hermit crab's behavioral choice to maximize the expected reproductive success, that is, on the decision about whether the individual chooses the behavior to seek and change its shell to a new one or not, which is assumed to correlate positively to the reproductive success. In this reason, we assume that the purpose of the behavioral choice about the shell change is to maximize the reproductive success in the subsequent breeding season. So we construct our model with the above-mentioned inter-breeding season, although its given constant length T is a mathematical simplification in our modeling.

When an individual with body size x tries to change the shell to another larger one, the probability that the individual succeeds in getting a larger shell is assumed to be given by φ. For mathematical simplification and clarification of our arguments, we assume that the probability φ is constant independently of the body size, although it may generally a function of body size x. Thus, the probability that the individual fails to get the larger shell is given by $1-\varphi$. We ignore the handling time for the shell change in our modeling. So, a shell change is assumed to occur at a moment in the inter-breeding season if it is successful.

2.3. Energy reserve

For our mathematical modeling, we define the *energy reserve* of individual. The energy reserve changes due to the energy input and output by feeding and homeostasis etc., which in general depend on the body size. We assume that the greater energy reserve at the beginning of the breeding season promises the greater reproductive success in the breeding season. Since the behavioral choice in the inter-breeding season can significantly affect the energy reserve, the individual should choose the behavior to make the energy reserve as much as possible at the beginning of the